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Short title: Nutritional Ecology of Bornean Orangutans

ABSTRACT

The spatial and temporal variation in food abundance has strong effects on wildlife feeding and nutrition. This variation is exemplified by the peatland forests of Central Kalimantan, which are characterized by unpredictable fruiting fluctuations, relatively low levels of fruit availability, and low fruit periods (<3% of trees fruiting) that can last nearly a year. Challenged by these environments, large, arboreal frugivores like orangutans must periodically rely on non-preferred, lower-quality foods to meet their nutritional needs. We examined variation in nutrient intake among age-sex classes and seasons over a 7-year period at the Tuanan Orangutan Research Station in Central Kalimantan. We conducted 2,316 full-day focal follows on 62 habituated orangutans (*Pongo pygmaeus wurmbii*). We found differences in total energy and macronutrient intake across age-sex classes, controlling for metabolic body mass. Intake of both total energy and macronutrients varied with fruit availability, and preference of dietary items increased with their nutritional quality. Foraging-related variables, such as day journey length, travel time, and feeding time, also varied among age-sex classes and with fruit availability. Our results add to the growing body of literature suggesting that great variation in foraging strategies exists among species, populations, and age-sex classes and in response to periods of resource scarcity.

KEYWORDS: energetics, peatland, Borneo, food preference, fallback foods, nutrition, orangutans

INTRODUCTION

Spatial and temporal variation in food abundance influences wildlife feeding behavior and nutrition, and ultimately fitness. This variation can lead to changes in vulnerability to predation, shifts in ranging patterns, reproductive seasonality, changes in feeding efficiency and physical condition, all of which have implications for overall population abundance [McNamara and Houston, 1987]. For example, reindeer change their ranging patterns and experience a reduction in body condition during periods of food scarcity in the winter months, which in turn affects their vulnerability to predation [Tablado et al. , 2014]. Black bears digest food more efficiently in the months just before denning, and gain weight rapidly as an adaptation to seasonality [Brody and Pelton, 1988; Shimozuru et al. , 2012]. Several primate species restrict their breeding season to coincide with periods of high food abundance, thereby enhancing overall fitness [reviewed in Brockman and van Schaik, 2005]

The great majority of primates are confined to tropical and subtropical forests [Mittermeier, 1988; Richard, 1985], which are characterized by variation in both the temporal and spatial availability of preferred food resources, including fruits, leaves, and flowers [Janson and Chapman, 1999; van Schaik and Pfannes, 2005; van Schaik et al. , 1993]. Southeast Asian forests exhibit greater variability in fruit production than African forests [van Schaik and Pfannes, 2005]. The better known masting forests of Southeast Asia, dominated by Dipterocarpaceae, are characterized by dramatic supra-annual peaks in flower and fruit availability [Ashton et al. , 1988; Cannon et al. , 2007b; Curran and Leighton, 2000; van Schaik, 1986], overall low fruit productivity [van Schaik and Pfannes, 2005], and irregular and unpredictable fruit production [Ashton et al. , 1988; Wich and van Schaik, 2000]. In contrast, the non-masting peatland forests of Central

Kalimantan, which hold the largest remaining populations of orangutans in Indonesia [Ancrenaz, 2007; Morrogh-Bernard et al. , 2003; Wich et al. , 2008], show less pronounced fluctuations in fruit availability relative to masting forests [Cannon et al. , 2007a; Wich et al. , 2011].

Most frugivorous primates exhibit a diverse array of strategies to cope with meeting energetic needs during periods of fruit scarcity [van Schaik and Brockman, 2005; van Schaik et al. , 1993]. The most common of these strategies involves dietary switching to alternative, less preferred resources [Hemingway and Bynum, 2005; Lambert and Rothman, 2015; Marshall and Wrangham, 2007] in an attempt to maximize energetic gains while simultaneously minimizing the energetic costs of foraging. This dietary switching is a common strategy across orangutan population [Morrogh-Bernard et al. , 2009; Russon et al. , 2009].

Few published studies have examined the nutritional ecology of orangutans across an extended period encompassing several cycles of fluctuating fruit availability [but see Vogel et al. , 2015]. Knott [1998] investigated the nutritional ecology of Bornean orangutans in a lowland dipterocarp forest during a one-year period that included a masting event followed by a low fruit period. She found that during the low-fruit period both adult males and females had significantly lower caloric intake compared to the high-fruit mast period and that males consumed more calories than females; but during the high-fruit period, caloric intake did not differ between the sexes [Knott, 1998]. In contrast, in a peat-swamp habitat, Harrison and colleagues [2010] found that fruit availability and daily caloric intake were positively correlated for flanged males only, and the relationship was weaker than that found in the masting forest [Harrison et al. , 2010].

This reduced energy intake during low fruit periods resulted in flanged males often falling below the estimated energy requirements [Harrison et al. , 2010].

Given this variation between the sexes, it is important to examine how difference in orangutan energetic demands may influence their energetic strategies. One factor that may influence energetic demands is body size [Gaulin, 1979]. Adult male orangutans are characterized by bimaturism: flanged males are typically at least twice the size of adult females, whereas the growing, unflanged males start out at the same size as adult females [Dunkel et al. , 2013; Harrison and Chivers, 2007; Utami et al. , 2002]. Thus, flanged males likely have higher maintenance requirements compared to adult females and unflanged males; however, because metabolic costs are a function of body mass (e.g., $M^{0.73}$), adult flanged males' nutritional needs per kg of body mass should be lower compared to smaller females, unflanged males, and immature males and females. The metabolic demands of pregnancy and lactation are also expected to be high for adult females, given that they are nearly always either pregnant or lactating [Knott, 1999; Knott et al. , 2009; van Noordwijk et al. , 2013]. Likewise, immatures have greater nutritional needs per unit body mass to sustain body mass accumulation during this period of growth and development [Oftedal, 1991; Rothman et al. , 2008]. These higher nutritional demands combined with a higher relative metabolic rate for smaller individuals could result in adult females and juveniles consuming more food per kilogram of body mass compared to larger flanged males. Because unflanged males are still growing and smaller than flanged males [Dunkel et al. , 2013], their nutritional demands per kg body mass are likely to be greater than flanged males but lower than immatures. Although they these unflanged males are still investing energy into growth, their

energetic demands are likely lower than lactating or pregnant adult females, despite similarities in body size. However, because we know very little about the energetic costs associated with transitioning to the flanged male state, predictions regarding differences among unflanged males and females are tentative.

Here we examine variation in orangutan nutritional intake and related foraging behaviors among immature males and females, adult females, flanged males, and unflanged males in a peatland habitat across a seven-year period. While previous studies have examined variation in energy intake among adult orangutans, they have not included independent immatures in their comparisons. We controlled for metabolic body mass to consider variation in nutritional intake among age-sex classes on an equivalent basis [Rothman et al. , 2008]. We tested the following hypotheses:

1. Total energy and macronutrient intake vary among age-sex classes. Due to their larger bodies and absolutely greater nutritional needs, flanged males will have the greatest energy intake. Adult females and unflanged males should have more equivalent intake. However, controlling for metabolic body mass, flanged males should have the lowest energy and macronutrient intake and immature males and females should have the highest, followed by adult females and unflanged males based on their metabolic energetic requirements.
2. Activity patterns influencing energetics vary among age-sex classes. We predicted that flanged males would have the shortest active periods and day journey lengths, and spend the least time feeding and traveling [Morrogh-Bernard et al. , 2009; van Schaik et al. , 2009]. We predicted that immature males and immature females would have the longest day journey lengths and would spend more time feeding, as they

have the greatest nutritional needs and are establishing home ranges. Because unflanged males range over large areas [Singleton et al. , 2009; Singleton and van Schaik, 2001], we predicted their day journey lengths would be between flanged males and immature individuals. Due to the energetic demands of lactation and gestation, we predicted that adult females would spend more time feeding than flanged and unflanged males, but less than immature individuals.

3. Both time spent traveling and day journey length increase with increasing fruit availability [Wartmann et al. , 2010]. This hypothesis is based on previous observations that orangutans include a greater proportion of fruit in their diets when fruit is available [Knott, 2005; Vogel et al. , 2015; Wich et al. , 2006]. Because fruiting trees are often widely spaced, greater travel distances are expected during high-fruit periods relative to low-fruit periods, when they are consuming bark and leaf resources [Vogel et al. , 2008]. In addition, because they are traveling more, they are likely to have longer active periods and/or spend less time feeding when fruit is abundant, as fruit energy can be more efficiently harvested.
4. Macronutrient and energy intake vary with the availability of fruit. Specifically, we predicted that daily energy, non-structural carbohydrates, and dry matter intake are positively related to fruit availability. On the other hand, protein intake should be negatively related to fruit availability, as leaves are generally higher in protein compared to fruit [Conklin-Brittain et al. , 2006; Rothman et al. , 2011] and Tuanan orangutans consume leaves as fallback foods [Vogel et al. , 2008].
5. Orangutans preferentially select food characterized by the greatest energy returns. Previous studies have demonstrated that orangutans prefer fruit and tend to consume

leaves, inner-bark, and flowers when fruit is not available [Bastian et al. , 2010; Harrison et al. , 2010; Knott, 1998; Morrogh-Bernard et al. , 2009; Vogel et al. , 2009]. We predicted that fruits would be preferred and provide the greatest energetic return, and leaves and inner-bark would be least preferred with lower energetic returns.

METHODS

Study Site and Subjects

Data were collected in the Tuanan Orangutan Research Station area (2°09' S and 114°26' E) in Central Kalimantan, Indonesia. Tuanan comprises and is located in the 3,090 km^2 Mawas Conservation Area, along the Kapuas River [van Schaik et al. , 2005] and comprises approximately 900 ha of peat swamp forest with a peat depth of 1-2 m in most parts (overall depth of $\leq$ 3.5 m) [Alavi, unpublished data].

Tuanan's orangutan population density is estimated to be between 4.3 and 4.5 individuals/km^2 [Husson et al. , 2009; van Schaik et al. , 2005], among the highest in Borneo [Husson et al. , 2009]. For this study, we collected data from 62 known individuals (adult females (AF) = 14; flanged males (FLM) = 26; unflanged males (UFM) = 9; independent immature females (IF) = 7; independent immature males (IM) = 6). We only included individuals that ranged independently of their mothers, and considered females as immatures until they had their first offspring, and males when they reached adult female body size.

Behavioral Data Collection

Behavioral data were collected following standardized protocol (http://www.aim.uzh.ch/de/research/orangutannetwork/sfm.html) and only data collected during full nest-to-nest follows were included in each analysis [van Schaik, 1999]. Activity and feeding data were collected during 2-minute instantaneous samples. For feeding bouts, we recorded the species, plant part, and stage of ripeness of foods. We calculated total minutes per day spent moving as well as feeding on each food (species/item). Feeding and nutritional analyses were based on 24,645 observation hours and 14,270 hours of feeding collected from July 2003 through August 2010 (see SI Table I for a breakdown of the number of focal follows for each age-sex class). Moving, active period, and ranging analyses were based on 28,000 hours of data collected between July 2003 and July 2012. We defined *active period* as the duration (minutes) between when an individual left the nest in the morning until it settled into its night nest. Feeding rates (number of items - or area of cambium and phloem for bark- consumed per minute) [cf. Knott, 1998] were collected opportunistically during feeding bouts between 2003 and 2012 and were averaged for each age-sex class for calculations of macronutrient and energy intake [Vogel et al. , 2015]. To calculate the percentage of time spent feeding on each food items (e.g., leaf, fruit, bark, etc.), we divided feeding minutes on each item by total feeding time for each full-day focal follow.

For day journey length (DJL), the total distance an animal traveled during the day, we used two different protocols. Prior to 2007, each focal animal's path was hand-drawn on a map of the study grid with trails marked at 50-meter intervals using a compass. These maps were then digitized and the polyline distance was calculated to determine DJL [see Wartmann et al. , 2010 for full description]. After 2007, handheld Garmin GPS

units were used to record the location of the focal animal. For both methods, locations were recorded every 30 minutes. DJL was calculated from these data in ArcGIS (ESRI, Redlands, CA, USA). Wartmann [2008] compared simultaneously collected GPS and hand-drawn map data and found that they did not significantly differ.

Observational protocols were approved by IACUC committees of UC-Santa Cruz (protocol #20061056-122204) the George Washington University (protocol #A186), and Rutgers University (protocol #11-030). Our research complied with the American Society of Primatology Principles for the Ethical Treatment of Non-Human Primates.

Ecological Data Collection

Fruit availability

Fruit availability was determined each month by monitoring phenology plots containing 1,868 tagged trees covering 2.3 ha, which were spread across the home ranges of the most heavily sampled individuals in our dataset [Vogel et al. , 2008]. All trees with a diameter at breast height (DBH) of >10 cm were monitored each month for the presence of unripe, half-ripe, and ripe fruit [as in Vogel et al. , 2008]. To estimate fruit abundance, we calculated the fruit availability index (FAI) as the percentage of fruiting trees in the phenology plots each month (SI Fig.1) [Vogel et al. , 2008; Wrangham et al. , 1998]. High-, medium-, and low-fruit periods were determined by calculating the statistical quartiles for data pooled across the study period. In addition to monitoring fruit availability in phenology plots, we also recorded the monthly presence of flushing leaves and flowers for each species and used these data to calculate selectivity/preference scores.

Plant sample collection and nutritional intake calculations

Food samples for this study were collected between June 2004 and September 2011 [see Vogel et al. , 2015 for a description of sample collection methods]. All nutritional analyses were conducted in the Laboratory of Nutrition Testing in the Research Center for Biology at the Indonesian Institute of Sciences (LIPI) following standard techniques [Harrison et al. , 2010; Vogel et al. , 2015]. We followed the nutritional methods and energetic calculations reported by Vogel and colleagues [2015], with the acceptation of estimating available protein. We were unable to conduct available protein analyses for this study because this analysis was not available in Indonesia and export permits could not be obtained. Thus, we estimated available protein from crude protein values by using conversion coefficients for similar food items from Indonesia [Conklin-Brittain et al. , 1999]. We realize this is not ideal, but since similar foods are sampled, our available protein estimates may only slightly over- or underestimate actual available protein. All nutritional results are reported as 100% dry matter (DM) [Conklin-Brittain et al. , 2006].

Energy intake per feeding bout was calculated following Vogel et al. [2015]. Feeding bouts were summed across each follow day to obtain total daily caloric intake (Kcal). If nutritional data and/or feeding rates were not available for a given plant species, we used 1) values from a different species within the same genus with similar fruit size/character or, if this was not available, 2) the average value for that item (fruit, leaves, inner-bark, flowers, vegetation) and stage of ripeness across all food species When available, we used sex-specific feeding rates for each species. However, when these data were not available for a given sex, average feeding rates obtained for the other

sex were used, as Vogel and colleagues [2015] found that feeding rates do not differ between sexes,

Body Mass and Energy Requirements

To test the hypothesis that nutrient intake differs among age-sex classes, we calculated macronutrient and energy intake in two ways. First we calculated how much each orangutan consumed on an absolute basis. Second, we divided these absolute estimates of daily energy and macronutrient intake by the estimated metabolic body mass (MBM) for each age-sex class, using a scaling exponent of 0.73 [following Pontzer et al. , 2014]. Because there are few published values for wild Bornean orangutan body mass [Markham and Groves, 1990; Rayadin and Spehar, 2015], we used a combination of published and unpublished data to derive body mass estimates. For adult flanged males and adult females, we used Markham and Groves' [1990] published values of 86.3 kg and 38.8 kg, respectively [following Harrison et al. , 2010]. The only published values for unflanged adult males is 40.5 kg (range 28-58) [Rayadin and Spehar, 2015], and while this value is for *Pongo pygmaeus morio* in a disturbed habitat and thus may be low, we opted to use this value instead of visually estimating. For independent immature males and females, we used unpublished data collected from wild-caught individuals upon their arrival at the Borneo Orangutan Survival Foundation's orangutan rehabilitation center at Nyaru Menteng. We classified individuals from this database as immature if they were estimated at 6-14 years of age and did not have an erupted M3 [Smith, T.M., *pers.com*]. In the Tuanan population, individuals are typically completely weaned by 6.5 years of age [van Noordwijk et al. , 2013] and females' age of first reproduction is typically

around 15 years [Wich et al. , 2009]. Using these criteria, we assigned immature females the average weight of 22.7 kg (range 15-30 kg; n=12) and immature males the average weight of 28.9 kg (range 22–37 kg; n=6) [Borneo Orangutan Survival Foundation, unpublished data].

To estimate daily energy expenditure (DEE; kcal/d), we used published data from four captive orangutans for which DEE was measured using doubly labeled water [Table 1 in Pontzer et al. , 2010] to calculate the regression equation: DEE (kcal/d) = $439.32*(\text{body mass (kg)})^{0.324}$, $r^2=0.99$. We entered the body mass estimates for each age-sex class into this equation, which resulted in the following expected DEE's: 1,207 kcal for immature females, 1,306 kcal for immature males 1,435 kcal for adult females, 1,456 kcal for adult unflanged males, and 1,861 kcal for adult flanged males. To estimate the costs of lactation, we followed Knott [1999] and estimated lactation costs for adult females as 1.5 * DEE resulting in 2153 kcal (717 Kcal increase)[Coelho, 1974; Coelho, 1986]. These estimates, with the exception of adult females, are lower than estimates used by Harrison and colleagues [2010], who used a standard equation derived for all primates [Key and Ross, 1999], which was modified by decreasing the resulting values by 10% to account for reductions in energy expenditure in orangutans (see Table III for a comparison).

Preferred and Fallback Foods

We follow Marshall and Wrangham's [2007] definition of fallback foods as items whose consumption is negatively correlated with the availability of preferred foods. While we cannot truly know food 'preference' of the orangutans, we can apply a measure

of selectivity as a proxy. Following Bastian et al. [2010], we calculated Vanderploeg and Scavia's [1979] selectivity coefficient for all foods (species-item), as this index treats rare and common items in the habitat more evenly than other indices [Lechowicz, 1982]. The index is calculated as:

$$\frac{r_i/p_i}{\sum_i(r_i/p_i)}$$

where r_i = the proportion of food item i in the diet based on feeding times calculated from feeding data, and p_i = the proportion of food species/item i in the environment, estimated from monthly phenology plots [see Bastian et al. , 2010 for details]. For example, if the orangutans were consuming flowers of a given species that month, we calculated the proportion of trees baring flowers of that species across all tree species in the plots. For the fruits of non-woody vegetation, including lianas, we monitored ten 10x 10m plots spread randomly across the study area for 12 months (2009 to 2010). The index was calculated separately for each age-sex class category. We did not distinguish between mature and young leaves because observers did not record leaf maturity consistently. We separated non-fig fruits from figs (*Ficus spp.*), as previous studies have found that figs are commonly used as fallback foods by primates in Southeast Asia [Marshall et al. , 2009; Marshall and Leighton, 2006]. Because phenological data were calculated on a monthly basis, the index was calculated separately for each month.

Statistical Analyses

For all energy and macronutrient intake estimates, we excluded outlying data points that were more than 3 S.D. from the mean, resulting in the exclusion of 29 of 2,322 follows. To examine variation in total energy and macronutrient intake among age-

sex classes, generalized additive mixed models (GAMM) were run using the MGCV package in R [R Developement Core Team, 2015; Wood and Wood, 2015]. GAMMs are semi-parametric extensions of generalized linear models where the linear predictor involves a sum of smooth functions of the predictor variables, smooth terms are represented using penalized regression splines, and inference is based on these smooth functions [Hastie and Tibshirani, 1986; Hastie and Tibshirani, 1990; Wood, 2006a]. For further information on how we calculated smooth functions, see Wood [2006b]. Individual ID was included as a random effect in each model and to minimize type 1 errors we included random slopes in the models, and thus all models are fully maximal [Barr et al. , 2013].

For models that included FAI as a predictor variable, we took advantage of MGCV's factor-by-variable feature to allow the smooth of FAI to interact with age-sex class. This was important as it provided us with a method to examine whether FAI varied with the dependent variable across all age-sex classes. Models run with and without interaction terms were compared and model selection was based on Akaike Information Criterion (AIC) and adjusted R-squared values [Akaike, 1974; Wood, 2006a; Wood, 2006b]. In addition, for models that included FAI as a predictor variable, we used absolute intake and did not control for MBM, as we were concerned with how nutrient intake varied with FAI and not with differences among the age-sex classes as in prior analyses. However, age-sex class and the interaction term of age-sex class by FAI were included in these models as independent variables.

Kruskal-Wallis tests and multiple comparisons were used to further explore overall age-sex class differences when GAMMs were significant, though because the

Kruskal-Wallis test cannot incorporate random effects or include multiple fixed effects, Kruskal-Wallis results may differ from GAMM results. This provided us with additional information regarding the direction of differences among the age-sex classes, something the GAMMs do not indicate. We performed multiple comparisons tests [Siegel and Castellan, 1988] using the package pgirmess [Giraudoux and Giraudoux, 2015]. We applied the Holm-Bonferroni correction for multiple comparisons [Holm, 1979]. We set the significance level for all tests at $\alpha < 0.05$ and noted trends toward significance ($0.05 < p < 0.10$). All statistical procedures were carried in R [The R Foundation for Statistical Computing: http://www.R-project.org].

RESULTS

Age-Sex Class Variation in Energy and Macronutrient Intake

With the exception of daily protein intake, there were no differences among age-sex classes in absolute macronutrient or energy intake. Once we controlled for MBM, however, differences among the age-sex classes emerged in total energy intake and macronutrient intake (Table I; Fig. 1). Below, we report the results controlling for MBM, unless noted. As predicted, flanged males had lower energy intake compared to all other age-sex classes, whereas immature females had higher energy intake compared to all other age-sex classes except immature males. Energy intake did not differ between adult females and unflanged or immature males, but immature males had higher intake than unflanged males (Table I; Fig. 1a).

---INSERT TABLE I AND FIGURE 1 HERE---

Total non-structural carbohydrate (TNC) intake followed a similar pattern, exhibiting differences in all pair-wise comparisons of age-sex classes except between adult females and unflanged males or immature males, and between immature males and females (Table I, Fig. 1b). For TNC, flanged males again had the lowest intake and immature males and females had the highest, although immature males did not differ from adult females (Table I). For available protein intake, the models including and excluding MBM were both significant, although the explanatory power of the model including MBM was greater (Table I, SI Table III). Controlling for MBM, all age-sex class comparisons differed except those among adult females, unflanged males, and immature males (Table I, Fig. 1c). Overall, flanged males had the lowest protein intake and immature females had the highest. Lipids and NDF followed similar patterns: flanged males had lower intake and immature females had higher intake, with the exception of immature males, than all other age-sex classes. Whereas for lipids, there were no differences among adult females, unflanged males, and immature males; for NDF, immature males had higher intake than unflanged males (Table I, Fig. 1d, e). We also examined overall dry matter intake and found differences among all age-sex classes with the exception of adult females compared to unflanged males and immature males compared to immature females. Again, immature males and females had the highest dry matter intake and flanged males the lowest (Table I; Fig. 1f). In sum, when controlling for MBM, the largest age-sex class (flanged males), had the lowest energy and macronutrient intake while the smallest age-sex classes (immature males and females) had the greatest.

We examined the hypothesis that this variation in energy and macronutrient intake among age-sex classes is a consequence of differences in the amount of time spent in daily activities related to foraging and energetics. Flanged males had a shorter active period relative to all other age-sex classes except for immature males (Table II, Fig. 2a). Unflanged males' active periods were longer than any other age-sex class, followed by immature females, who differed from all sex-age classes except immature males (Table II, Fig. 2a). On a daily basis, immature females traveled farther than any other age-sex class except immature males, while flanged males had shorter day journey lengths compared to all age-sex classes except immature males (Table II, Fig. 2b). In terms of the amount of time spent traveling, immature females also spent the most time traveling on a daily basis, although they did not differ from immature males (Table II, Fig. 2c). However, our sample size for immature males was low, resulting in a large range and standard error, and thus reducing the power for comparisons with this age-sex class. Total daily feeding time (min) did not differ across the age-sex classes (Table II, Fig. 2d).

---INSERT TABLE II AND FIGURE 2 HERE---

The Effect of Fruit Availability on Daily Energy and Macronutrient Intake

The availability of fruit (FAI) at Tuanan fluctuated between <1% and 14% of trees fruiting, with fruiting peaks typically occurring between September and January and fruiting troughs between April and August (SI Fig. 1). This resulted in great variation in the intake of total energy and macronutrients across the study period (Table III). On average, flanged males fell below the estimated DEE in 19% of the months sampled, unflanged males in 11%, adult females in 19% (after accounting for estimated reproductive costs), immature males in 14%, and immature females in 7% (Table III).

---INSERT TABLE III HERE---

Overall, there was a positive relationship between energy intake (kcal/day) and FAI (SI Table II, Fig. 3a). Further model exploration revealed that this positive relationship held for all age-sex classes except for flanged and unflanged males, whose energy intake was not related to FAI (SI Table II, Fig. S2a). TNC intake also increased with FAI (SI Table II, Fig 3b) for all age-sex classes except flanged and immature males (SI Table II, SI Fig. 2b). While the model for protein intake was significant, this was driven by age-sex class differences and not by the availability of fruit (SI Table II); overall, there was no relationship between protein intake and FAI (Fig. 3c). However, for adult females and unflanged males, protein intake increased as FAI decreased (SI Table II, SI Fig. 2c). Lipid intake increased with FAI overall (Fig. 3d; SI Table II) for all age-sex classes except for immature and flanged males (SI Table II, SI Fig. 2d). NDF and dry matter intake were both positively related to FAI (Fig. 3e-f, SI Table II), and this relationship was significant for all age-sex classes except for immature males for NDF and all male age classes for dry matter (SI Table II).

---INSERT FIGURE 3 HERE---

Given that orangutans increased their energy and dry matter intake when FAI was higher, we examined whether daily behaviors related to foraging also varied with FAI. Overall, Tuanan orangutans spent more time traveling with increasing FAI (Fig. 4a), and had longer day journey lengths (Fig. 4b; SI Table II). The relationship between travel time and FAI was consistent for all age-sex classes except flanged males, and all age-sex classes increased day journey length with increasing FAI (SI Fig. 3a, b). Active period also increased with increasing FAI (Fig. 4c, SI Table III), which held for age-sex classes

except flanged and unflanged males (SI Fig. 3c). This increase in active period was not a consequence of increased time spent feeding when fruit was more abundant, as there was a negative relationship between total feeding time and FAI (Fig. 4d, SI Table III).

---INSERT FIGURE 4 HERE---

Preferred and Fallback Foods

During the study period, Tuanan orangutans spent 59.2% and 2.45% of their feeding time on non-fig and fig fruits, respectively, but included young leaves (13.7%), flowers (8.6%), insects (5.3%), inner bark (3.9%), mature leaves (2.4%), and other vegetative matter (2.6%) in their diet. We observed a 31% reduction in fruit, a 9% increase in inner bark, and smaller increases in the consumption in all other items except insects during the low fruit periods (Table IV).

---INSERT TABLE IV HERE---

Our GAMM models on the same data set used by Bastian and colleagues [2010] but controlling for orangutan identification confirm their results: Tuanan orangutans selected fruit over all food items, followed by flowers, inner-bark, leaves, and other vegetation (see SI Table IV, Fig. 5a for summary of data). During feeding bouts, fruit provided higher energetic gains per minute than all other food items, followed by leaves (young and mature), flowers, inner bark and other vegetation, although the latter two did not differ (SI Table IV, Fig. 5b).

---INSERT FIGURE 5 HERE---

To determine which items were used as fallback foods, we examined the relationship between fruit availability and the percentage of time spent feeding on different food items. The percentage of non-fig fruits and insects in the diet were

positively correlated with FAI, while the consumption of mature leaves was not related to FAI, and thus these items are not considered fallback foods (SI Table V; Fig. 6). Inner bark, pith, young leaves, flowers, figs, and other vegetation all showed a significant negative relationship with FAI, and thus fit the definition of fallback foods (SI Table V; Fig. 6).

---INSERT FIGURE 6 HERE---

DISCUSSION

Understanding Variation Among Age-sex Classes

Remarkably, we found very little variation among age-sex classes in absolute daily intake of energy and most macronutrients. This finding, that orangutans have similar nutrient intake despite differences in body sizes and energetic demands stands in contrast to research on gorillas, in which silverbacks consume more energy and macronutrients than adult females and juveniles [Rothman et al. , 2008]. Our results are similar to those found for the more frugivorous chimpanzee, whose absolute daily caloric and macronutrient intake did not differ between adult males and females, although when accounting for body size, females had a higher intake of nonstructural carbohydrates [Pokempner, 2009]. Wrangham and Smuts [1980] suggested that the lack of differences in feeding time in chimpanzees might be a consequence of reduced feeding competition due to sexual segregation and fluid communities. Owing to their relatively solitary lifestyle, orangutans can avoid overt feeding competition, which may enable them to meet their nutritional goals more easily when resources are limited [Knott, 2005; Knott et al. , 2008; Utami et al. , 1997]. We did find that absolute protein intake varied among some age-sex classes, with unflanged adult males consuming the greatest amount of

protein. It is possible that unflanged adult males have higher protein intake to increase muscle mass while transitioning to the flanged male state [Dunkel et al. , 2013].

Our results support the hypothesis that age and sex influence macronutrient and energy intake in orangutans, once metabolic body mass is accounted for. Based on body mass alone (before accounting for MBM), flanged males are expected to consume about 1.8 times as much food as other adult classes, and 2.5 times more than immatures. However, flanged males did not consume more food or obtain more energy compared to other age-sex classes. Our prediction that immatures and adult females would have higher energy and macronutrient intake and flanged males would have the lowest daily intake of most macronutrients and total energy, once accounting for MBM, were largely confirmed.

In a study of orangutans in a peatland habitat type, Harrison and colleagues [2010] found that there was little variation in dry matter and energy intake among adult females, flanged males, and unflanged males, although they did not conduct statistical comparisons. In a masting forest, adult male orangutans consumed more calories than females in the high-fruit period, but not when fruit was scarce [Knott, 1998]. Although neither of these studies accounted for MBM in their analyses, our results are largely in agreement with respect to orangutan nutrition. Several other studies focusing on a variety of sexually dimorphic primate species have found that males consume more total food than females [Alberts et al. , 1996; Nakagawa, 2000; Rothman et al. , 2008], yet we did not observe this pattern for the Tuanan orangutans.

While flanged males are expected to have lower energy intake per kg of $M^{0.73}$, the question remains: why don't these larger flanged males have greater absolute caloric

intake? Flanged males spent the same amount of time feeding compared to other age-sex classes in this study, and previous research found no sex differences in feeding rates in this population [Vogel et al. , 2015]. Thus, unlike other studies, which found that males spent less time feeding but have higher intake rates compared to females [Alberts et al. , 1996; Nakagawa, 2000; Rothman et al. , 2008], in this study flanged males obtain fewer calories per unit of $M^{0.73}$ on a daily basis. Flanged males at Tuanan have shorter active periods, travel shorter distances, and spend less time overall traveling compared to the other age-sex classes, which may be a form of compensation for their lower relative energy intake. Ashbury et al. [2015] found that flanged males travel on the ground more often than females, resulting in faster and potentially more energy-efficient travel [Cant, 1987]. However, this ground travel accounts for only 5% of their active time and they are primarily foraging and feeding during this time. Overall, these results suggest that flanged males at Tuanan have adopted a strategy of energy conservation. However, recent studies have suggested that decreases in physical activity may not translate into lower daily energy expenditure [Pontzer et al. , 2012]. Thus, future research should explore interactions between physiology, activity, and the environment among these males.

In a nearby peatland habitat – Sabangau – there were no significant differences in travel distances among adult age-sex classes [Harrison et al. , 2010]. In Tuanan immature females' activity patterns are also interesting: they travel greater distances and have longer active periods during which they spend more time traveling and feeding than most other age-sex classes. These females are recently independent of their mothers but range largely within the territory of their natal matriline [van Noordwijk et al. , 2012]. There are a few reasons why these immature females may have longer active periods and spend

more time in these activities, particularly ranging: 1) they are still establishing their core home-ranges [van Noordwijk et al. , 2012; Wartmann et al. , 2010] and/or have less knowledge of tree fruiting patterns in these areas [Janmaat and Chancellor, 2010]; 2) they are more social and engaged in greater levels of sexual activity outside of their natal ranges [Ashbury et al. , 2013]; 3) they do not have the additional burden of an offspring that requires multi-year lactation and care [van Noordwijk et al. , 2013].

The Effect of Fruit Availability and its Energetic Consequences

The overall positive relationship between fruit availability and daily energy intake is in concordance with previous studies on orangutans in masting forests [Conklin-Brittain et al. , 2006; Knott, 1998]. However, this relationship was not consistent across all age-sex classes in Tuanan, a pattern also found in another peatland site (Sabangau) [Harrison et al. , 2010]. Knott [1998; 2005] found that caloric intake was greater during periods of high fruit availability for adult females, flanged males and unflanged males in Gunung Palung (GP), while in Sabangau, Harrison and colleagues [2010] found this relationship only held for flanged males, with flanged males falling below energy requirements. Harrison et al. [2010] hypothesized that the effects of fluctuations in fruit availability on energy intake in flanged males may be stronger compared to adult females because males have pressing social demands. Our results do not support this hypothesis, as we found that energy intake increased with fruit availability for adult females, but not for flanged males. Thus, even within similar habitat types,[Harrison et al. , 2016] great variation may exist in energetic strategies across populations [Vogel et al. , 2015].

The mean daily energy intake of Tuanan orangutans fell between Sabangau (lower) and GP (higher) [Harrison et al. , 2010; Knott, 1998]. Though caloric intake was highest for orangutans in GP, they experienced the greatest reduction in caloric intake during the transition from high to low fruit periods [55-76%: [Knott, 1998], compared to a 48% reduction in Tuanan and an 18% reduction in Sabangau [Vogel et al. , 2015]. Thus, fluctuations in energy intake are more pronounced in the masting habitat compared to peatland habitats, which may explain the stronger relationship between ketone production and fruit availability in GP compared to peatland habitats [Harrison et al. , 2010; Knott, 1998; Vogel et al. , 2014]. In Sabangau, orangutans experienced more prolonged periods of low energy intake and negative energy balance relative to Tuanan and GP [Harrison et al. , 2010; Knott, 1998; Vogel et al. , 2014]. Thus, it is likely that variation in energy intake is related to the duration and extremes of high or low fruiting periods at these sites [Ashton et al. , 1988; Leighton, 1993; Medway, 1972; van Schaik, 1986; Vogel et al. , 2015].

At Tuanan, we found that protein intake was not related to fruit availability. Even though Tuanan orangutans rely on young leaves, which are typically higher in protein compared to fruit, as fallback foods [Dominy and Lucas, 2001; Vogel et al. , 2015], they include a fairly constant amount of protein in their diets across seasons, similar to spider monkeys [Felton et al. , 2009]. This pattern is similar for orangutans in GP, where overall protein intake did not vary with fruit abundance [Knott, 1998] or was weakly positively correlated [Vogel et al. , 2012]. However, in Tuanan, for both adult females and unflanged males, protein intake was negatively correlated with FAI – a pattern expected with increased consumption of proteinaceous young leaves.

Similar to GP, we found a positive relationship between TNC, lipids, and NDF and FAI. In GP, there was a negative relationship between NDF and fruit availability [Knott, 2005]. Thus, it may be that fruits at Tuanan are higher in fiber. Finally, while both GP and Tuanan have a positive relationship between dry matter intake and fruit availability, in Sabangau no relationship was detected [Harrison et al. , 2010; Knott, 1998], suggesting that orangutans in Sabangau may face, on average, greater energetic challenges.

We found an increase in the amount of time spent traveling and distance traveled with fruit availability, a pattern found in other populations of orangutans [Galdikas, 1979; Knott, 1999; Knott, 2005], and other large-bodied primates, including chimpanzees [Boesch and Boesch-Achermann, 2000; Hasegawa, 1990] and gorillas [Ganas and Robbins, 2005; Goldsmith, 1999]. This suggests that this increase in available energy may afford individuals the energetic means to travel farther in search of high quality resources. Indeed, Tuanan orangutans spent less time feeding overall when fruit was abundant, and thus they obtained more calories with lower feeding time investment. This pattern has been demonstrated consistently in other orangutan populations [see Table 12.3, Knott, 2005]. However, this pattern is opposite to that of other primates, like the diademed sifakas (*Propithecus diadema*), which shows reduced feeding time in the low fruit period [Irwin et al. , 2015].

In some forests, orangutans seem to have a unique energetic strategy among apes: they take advantage of high fruit periods by building fat reserves when calorie-rich foods are most abundant, and catabolize these reserves during periods of energetic shortfall [Knott, 1998]. This adaptation to coping with extreme variation in fruit availability may

help explain why captive orangutans are especially prone to obesity and diabetes relative to other great apes [Gresl et al. , 2000; Zihlman et al. , 2011], as African tropical forests have less pronounced dry and wet seasons and lower inter-annual variation in fruit availability [van Schaik and Pfannes, 2005].

Variation in food availability has been shown to have profound effects on correlates of fitness such as growth, fecundity and survival of primates. In many primate habitats, seasonality strongly influences the timing of reproduction [Hemingway, 1999]. Saddle-back tamarins lose 5% of their body mass and do not breed during the dry season when fruits and insects are less abundant [Goldizen et al. , 1988]. Similarly, breeding in langurs (*Presbytis* spp.) coincides with the times when they are in best physical condition when higher quality food resources like fruit are available [Jin et al. , 2009; Koenig et al. , 1997]. Seasonal mortality is prevalent across primates, which may be related to the synergistic effects of nutritional stress and disease [Cheney et al. , 1981; Gogarten et al. , 2012; Milton, 1996; Milton and Giacalone, 2014; Rudran and Fernandez-Duque, 2003]. Orangutan reproduction may be somewhat buffered from fluctuations in fruit availability due to their multi-year lactation [van Noordwijk et al. , 2013], as the option of adjusting energy needs of reproduction to fruit abundance is not available. There is currently little evidence that the timing of wild female orangutan reproduction is affected by fruit availability, and recent research has shown that a mother's feeding time does not vary with infant age [van Noordwijk et al. , 2013]. More long-term studies with complete inter-birth intervals from Sumatra and Borneo are needed to examine the effect of fruit availability and energy intake on reproduction and fitness [Knott et al. , 2009]. Armed with a more nuanced understanding of the nutritional strategies of orangutans and other

primates, we will be better able to understand the ecological drivers of population abundance, sociality, and reproductive strategies.

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Figure 1: Violin plots of age sex class differences in intake of a: metabolizable energy; b: total nonstructural carbohydrates (TNC); c: available protein; d: lipids; e: neutral detergent fiber (NDF); and f: dry matter. The larger white violins in the background represent intake before accounting for metabolic body mass (MBM), while the filled violins in the foreground represent intake after accounting for MBM. The point-range and mean are indicated in the center of the foreground violins. The left y axis corresponds to intake before accounting for MBM, while the right y axis corresponds to intake after MBM. Violin plots are equivalent to boxplots but also show the kernalized distribution estimates, allowing for visualization of any potential multimodal distributions. See Table I for statistics.

Figure 2: Violin plots of age sex class differences in a: active period; b: daily journey length; c: travel time; and d: total feeding time. Each violin shows the kernalized distribution estimates with an overlaid box showing the interquartile range and a line indicating the mean. Violin plots allow for visualization of any potential multimodal distributions. See Table II for full model statistics.

Figure 3. Smoothed model terms from five GAMM outputs. a: total energy intake (whole model r^2_{adj}= 0.25, $F_{(6,2246)}$=225.74, p<0.0001); b: Total nonstructural carbohydrates (whole model r^2_{adj}= 0.27 $F_{(6,2246)}$=241.2, p<0.0001); c: Available protein (whole model r^2_{adj}= 0.16 $F_{(6,2246)}$=221.79, p<0.0001); d: Lipids (whole model r^2_{adj}= 0.13 $F_{(6,2246)}$=106.67, p<0.0001); e: Neutral detergent fiber (whole model r^2_{adj}= 0.23 $F_{(6,2246)}$=342.37, p<0.0001); and f: Dry matter (whole model r^2_{adj}= 0.27 $F_{(6,2246)}$=280.13, p<0.0001). Estimated effects (estimated smooth functions) are represented as solid lines, and the 95% Bayesian credible interval is represented as dashed lines. For both Figures 3 and 4: The y-axis scale is in response units (on the scale of the linear predictor), and the x-axis is the variable range. The y-axis label is the fitted function with the estimated degrees of freedom in parenthesis, and the rug plot at the bottom indicates sampled values of the covariates of each smooth. Plots of the estimated smooth functions for each individual factor level are included in the supplemental material. See SI Table IV for full statistical results including smooth and interaction terms.

Figure 4. Smoothed model terms from four GAMM outputs. a: active period (whole model r^2_{adj}= 0.09 $F_{(2,2205)}$=3145.33, p<0.0001); b: daily journey length (whole model r^2_{adj}= 0.15 $F_{(2,2037)}$=143.64, p<0.0001); c: travel time (whole model r^2_{adj}= 0.10 $F_{(2,2257)}$=133.14, p<0.0001); and d: total feeding time (whole model r^2_{adj}= 0.02 $F_{(2,2253)}$=464.69, p<0.0001). Estimated effects (estimated smooth functions) are represented as solid lines, and the 95% Bayesian credible interval is represented as dashed lines. Plots of the estimated smooth functions for each individual factor level are included in the supplemental material (SI Figure 3) and model outputs are included in SI Table V).

Figure 5. (a) Variation in preference using Vanderplog and Scavia's selectivity index among the major food items in the orangutan diet at Tuanan. There was significant variation in preference among items (GAMM: r^2_{adj}= 0.06, $F_{(3.395)}$=42.4, p<0.0001). Posthoc non-parametric multiple comparisons revealed that fruit (FR) was preferred than all other items, flowers (FL) over bark (BK), leaves (LV), and other vegetation (VEG), and bark was preferred to leaves (p<0.05). (b) Variation in energy intake (Kcal/min). There was significant variation among items (GAMM: r^2_{adj}= 0.21, $F_{(6.97)}$=812.6, p<0.0001), with a posthoc non-parametric multiple comparison revealing that fruit has a higher energetic return relative to all other items, flowers higher than bark, leaves, and other vegetation, bark high than leaves and vegetation, and leaves higher than vegetation (p<0.05). See SI Table VI for full-model results.

Figure 6. Linear representations of the relationship between the number of minutes per item and FAI for each type of dietary item. a) Inner-bark/cambium: r^2_{adj}=0.16, $F_{(2.84)}$=37.56, p<0.0001; b) Non-woody pith: r^2_{adj}=0.16, $F_{(3.55)}$=21.93, p<0.0001; c) Young leaves r^2_{adj}=0.12, $F_{(7.91)}$=22.72, p<0.0001; d) Non-fig fruit r^2_{adj}=0.18, $F_{(7.45)}$=40.39, p<0.0001; Mature leaves r^2_{adj}=0.01, $F_{(1)}$=3.37, p=0.07; Flowers r^2_{adj}=0.09, $F_{(5.23)}$=14.06, p<0.0001; Insects r^2_{adj}=0.02, $F_{(5.98)}$=3.85, p=0.002; Fig fruit (*Ficus spp.*) r^2_{adj}=0.03, $F_{(1)}$=20.69, p<0.0001. Statistics provided are the smooth terms for the model. See SI Table VII for additional model outputs.

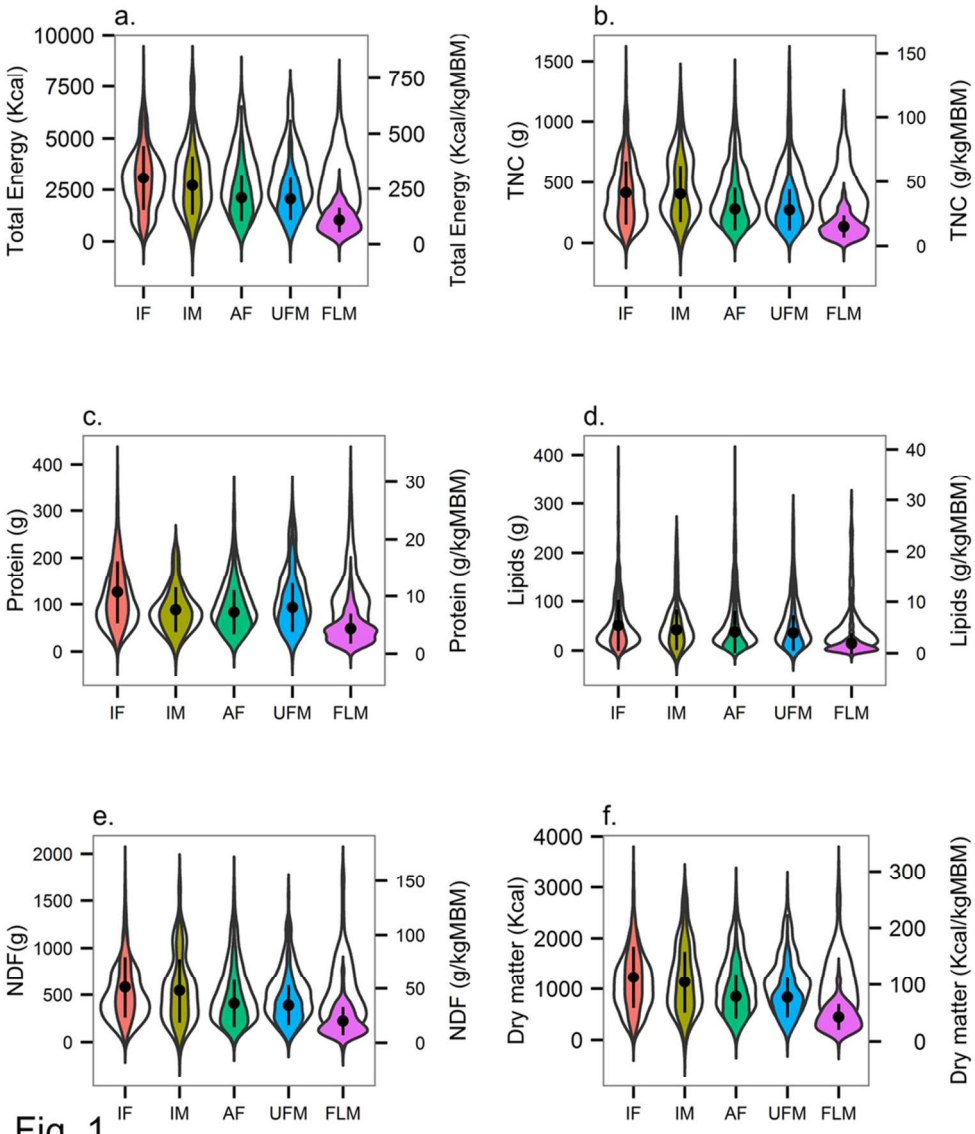

Fig. 1

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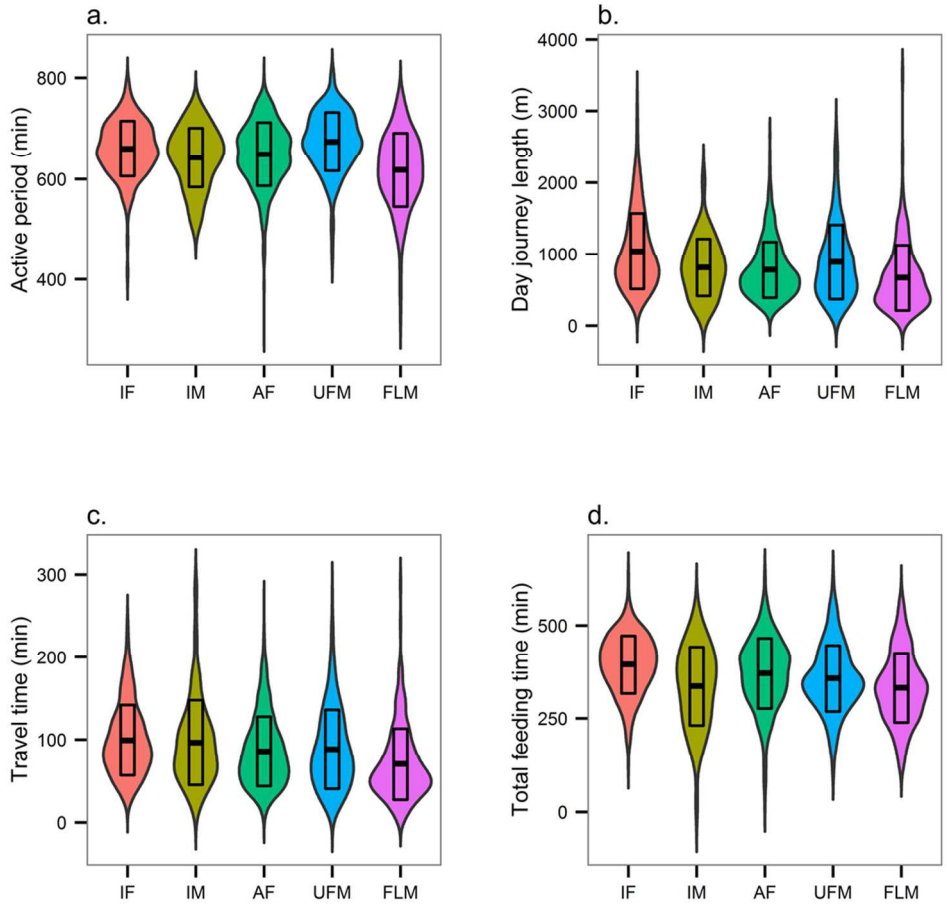

Fig. 2

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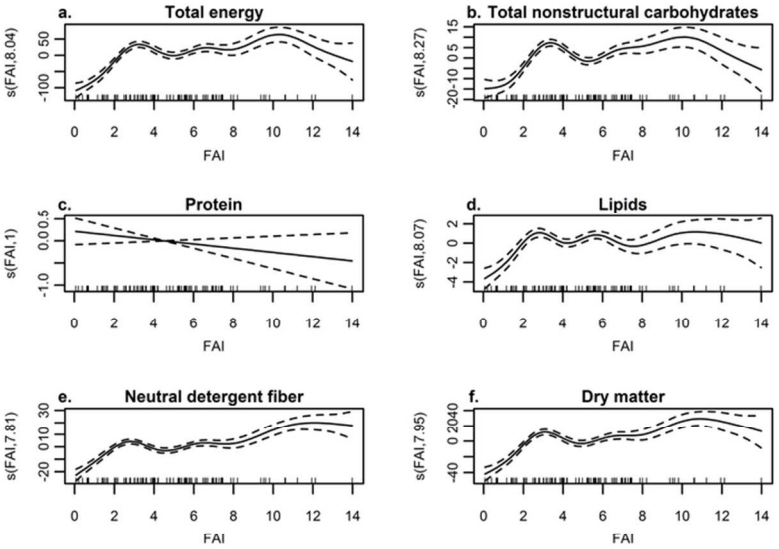

Fig. 3

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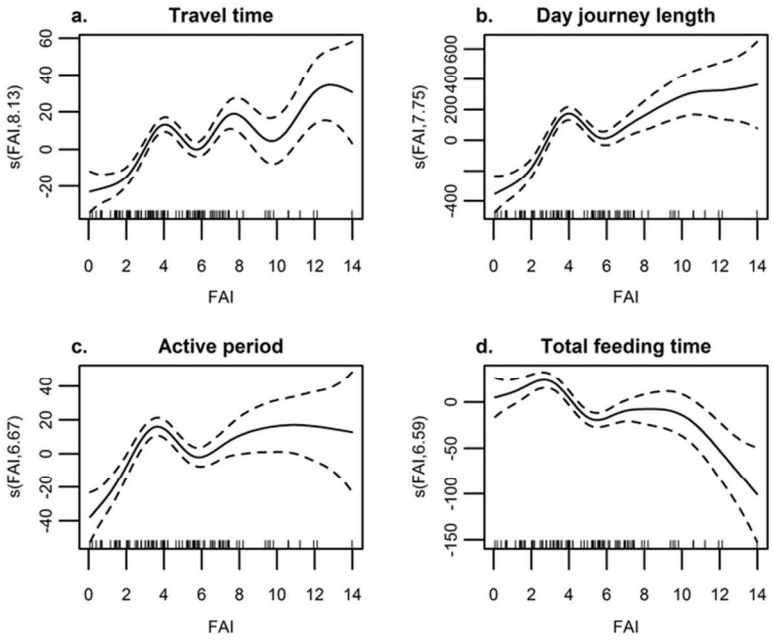

Fig. 4

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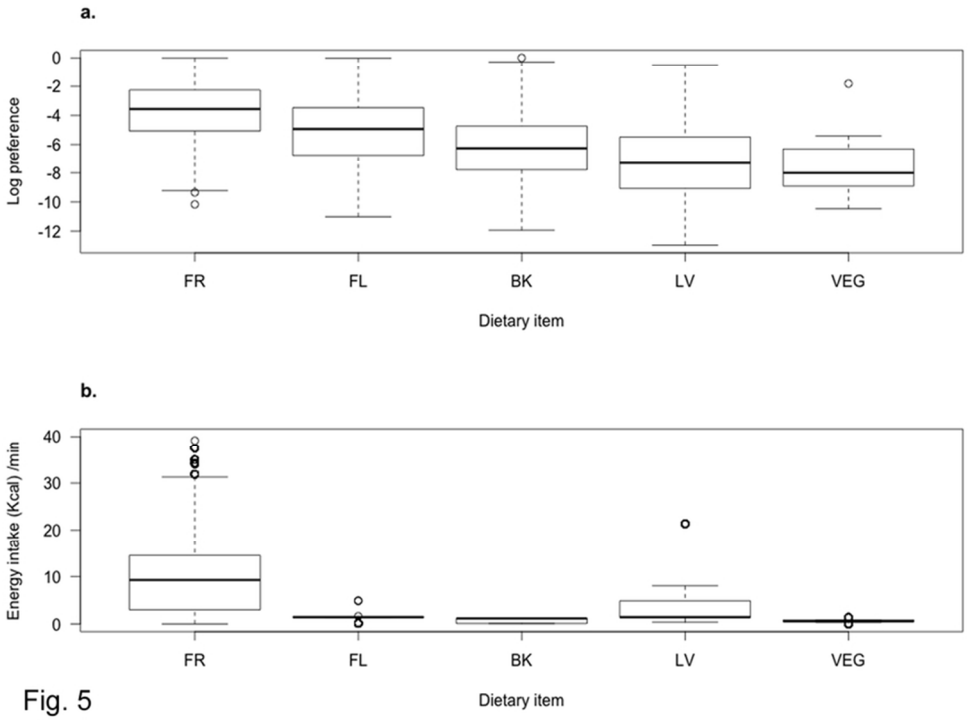

Fig. 5

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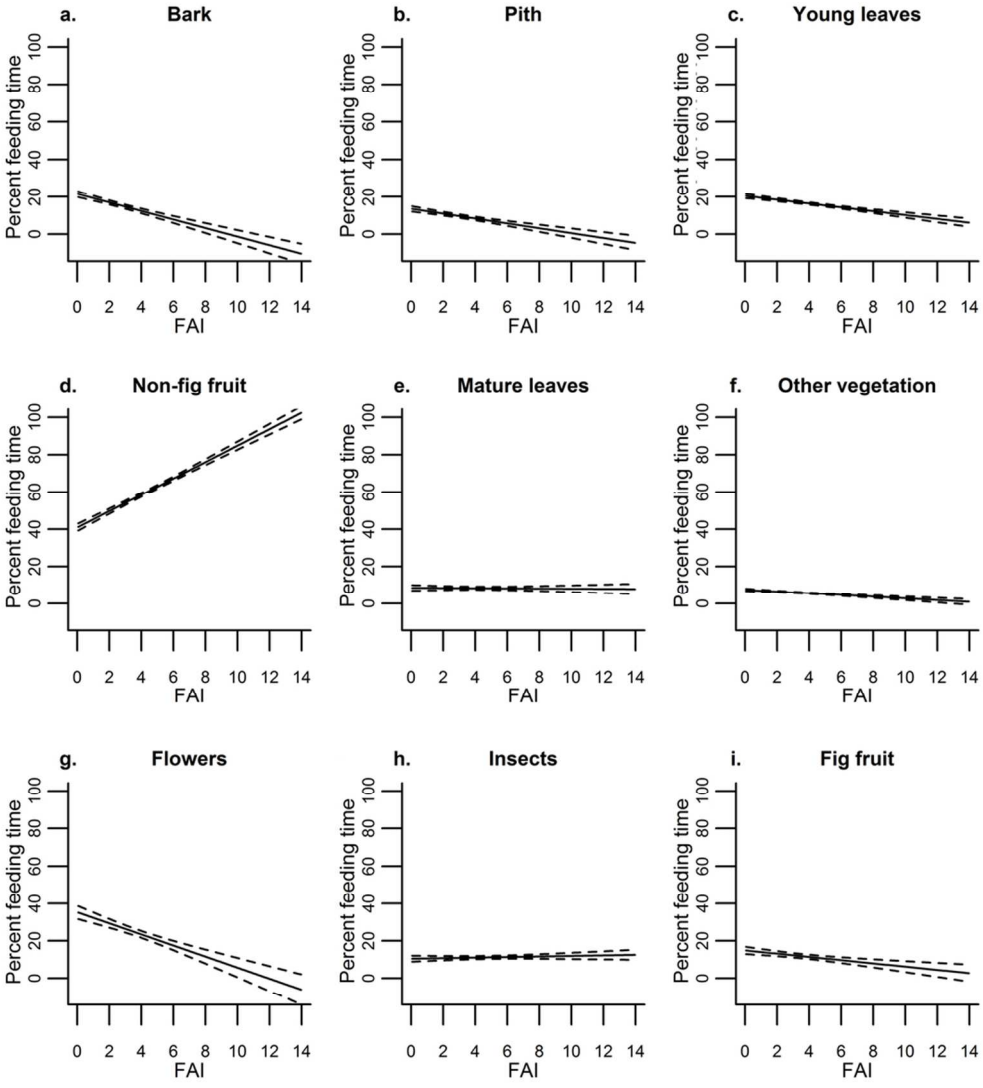

Fig. 6

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Table I: Variation among age-sex classes in daily intake of total energy (kcal) and macronutrients (g) with and without controlling for metabolic body mass (MBM). Data represent the mean ± SE. Non-parametric multiple comparisons were only preformed if the KW test was significant. GAMMs include orangutan ID as a random effect in the model and each data line represents a complete full-day follow. Random effect structure of each model is fully maximal. For a full breakdown of each variable see Table S2. For multiple comparisons, those comparisons in bold and with an asterisk (*) are significantly different after Bonferroni correction.

Age-sex class	Total energy		Available protein		TNC	
	kcal	kcal/kg MBM	g	g/kg MBM	g	g/kg MBM
Flanged male (FLM)	2801.86 ± 88.76	108.18 ± 3.43	67.27 ± 2.45	2.60 ± 0.09	386.89 ± 13.84	14.94 ± 0.53
Unflanged male (UFM)	3043.42 ± 96.43	204.14 ± 6.47	71.28 ± 2.42	4.78 ± 0.16	414.75 ± 16.23	27.82 ± 1.09
Adult female (AF)	3015.83 ± 40.80	209.11 ± 2.83	62.93 ± 0.89	4.36 ± 0.06	410.47 ± 6.36	28.46 ± 0.44
Immature male (IM)	3086.84 ± 202.93	264.95 ± 17.42	54.90 ± 3.59	4.71 ± 0.31	470.38 ± 33.76	40.37 ± 2.90
Immature female (IF)	2918.69 ± 71.96	299.03 ± 7.37	64.31 ± 1.65	6.59 ± 0.17	401.8 ± 12.22	41.16 ± 1.25
GAMM	r^2_{adj}= 0.001 $F_{(0.651)}$=0.252, p=0.19	r^2_{adj}= 0.18 $F_{(3.867)}$=49.17, **p<0.0001**	r^2_{adj}= 0.008 $F_{(2.46)}$=2.68, **p=0.002**	r^2_{adj}= 0.14 $F_{(3.672)}$=20.4, **p<0.0001**	r^2_{adj}= 0 $F_{(7e-06)}$=0, P=0.55	r^2_{adj}= 0.14 $F_{(3.845)}$=39.92, **p<0.0001**
KW test	χ^2= 5.15, df=4, p=0.27	χ^2= 399.31, df=4, **p<0.0001**	χ^2= 15.51, df=4, **p=0.003**	χ^2= 367.29,df=4, **p<0.0001**	χ^2= 6.10, df=4, p=0.19	χ^2= 316.95, df=4, **p<0.0001**
Multiple comparison		**AF-FLM***	AF-FLM	**AF-FLM***		**AF-FLM***
		AF-IF*	AF-IF	**AF-IF***		**AF-IF***
		AF-IM	AF-IM	AF-IM		**AF-IM***
		AF-UFM	**AF-UFM***	AF-UFM		AF-UFM
		FLM-IF*	FLM-IF	**FLM-IF***		**FLM-IF***
		FLM-IM*	FLM-IM	**FLM-IM***		**FLM-IM***
		FLM-UFM*	FLM-UFM	**FLM-UFM***		**FLM-UFM***
		IF-IM	IF-IM	**IF-IM***		IF-IM
		IF-UFM*	IF-UFM	**IF-UFM***		**IF-UFM***
		IM-UFM*	**IM-UFM***	IM-UFM		**IM-UFM***

Table I, continued:

Age-sex class	Lipid		NDF		Dry matter	
	g	g/kg MBM	g	g/kg MBM	g	g/kg MBM
Flanged male (FLM)	48.34 ± 3.28	1.87 ± 0.13	515.05 ± 20.70	19.89 ± 0.80	1105.55 ± 36.58	42.69 ± 1.41
Unflanged male (UFM)	58.32 ± 3.49	3.91 ± 0.23	514.67 ± 18.50	34.52 ± 1.24	1151.75 ± 35.84	77.25 ± 2.40
Adult female (AF)	59.53 ± 1.59	4.13 ± 0.11	521.44 ± 8.41	36.16 ± 0.58	1138.15 ± 15.23	78.92 ± 1.06
Immature male (IM)	52.87 ± 6.01	4.54 ± 0.52	559.30 ± 45.38	48.01 ± 3.89	1215.13 ± 82.82	104.30 ± 7.11
Immature female (IF)	52.63 ± 2.45	5.39 ± 0.25	500.82 ± 13.93	51.31 ± 1.43	1101.48 ± 26.78	112.85 ± 2.74
GAMM	r^2_{adj}= 0.003 $F_{(1.281)}$=0.727, p=0.07	r^2_{adj}= 0.05 $F_{(3.585)}$=14.28, **p<0.0001**	r^2_{adj}= 0 $F_{(9e-06)}$=0, p=0.50	r^2_{adj}= 0.12 $F_{(3.776)}$=27.85, **p<0.0001**	r^2_{adj}= 0 $F_{(1e-05)}$=233.62, p=0.43	r^2_{adj}= 0.17 $F_{(3.834)}$=39.31, **p<0.0001**
KW test Multiple comparison	χ^2= 13.13, df=4, p=0.01066	χ^2= 186.25, df=4, **p<0.0001** **AF-FLM*** **AF-IF*** AF-IM AF-UFM **FLM-IF*** **FLM-IM*** **FLM-UFM*** IF-IM **IF-UFM*** IM-UFM	χ^2= 1.59, df=4, p=0.8097	χ^2= 306.60, df=4, **p<0.0001** **AF-FLM*** **AF-IF*** AF-IM AF-UFM **FLM-IF*** **FLM-IM*** **FLM-UFM*** IF-IM **IF-UFM*** **IM-UFM***	χ^2= 2.85, df=4, p=0.5825	χ^2= 389.91, df=4, **p<0.0001** **AF-FLM*** **AF-IF*** **AF-IM*** AF-UFM **FLM-IF*** **FLM-IM*** **FLM-UFM*** IF-IM **IF-UFM*** **IM-UFM***

Table II: Variation in activities among age-sex classes. Data represent the mean ± SE (# of focal follows). For multiple comparisons, those comparisons in bold and with an asterisk (*) are significantly different after Bonferroni correction. GAMM models include Individual ID as a random effect and random effect structure in each model is fully maximal. Age-sex class abbreviations as in Table I.

Age-sex class	Active period (min)	Day journey length (m)	Travel time (min)	Feeding time (min)
FLM	618.29 ± 4.62 (259)	668.45 ± 32.25 (202)	70.14 ± 2.72 (250)	332.18 ± 5.81 (259)
UFM	674.34 ± 4.03 (217)	888.5 ± 36.27 (206)	88.24 ± 3.01 (253)	357.4 ± 6.03 (217)
AF	649.42 ± 1.69 (1396)	778.77 ± 10.98 (1280)	85.7 ± 1.08 (1514)	371.35 ± 2.52 (1396)
IM	642.72 ± 7.73 (58)	812.61 ± 64.82 (38)	96.47 ± 4.79 (115)	336.52 ± 13.89 (58)
IF	660.59 ± 2.81 (392)	1040.32 ± 27.61 (367)	99.29 ± 1.92 (493)	394.6 ± 3.93 (392)
GAMM	$F_{(4,2274)}$=1.838, **p=0.0157**	$F_{(4,2093)}$=4.065, **p<0.0001**	$F_{(4,2625)}$=0, **p<0.0001**	$F_{(4,2322)}$=102.19, p=0.565
KW test	χ^2= 95.39, df=4, **p<0.0001**	χ^2= 114.59, df=4, **p<0.0001**	χ^2= 98.08, df=4, **p<0.0001**	χ^2= 92.428, df=4, p<0.0001
Multiple comparison	**AF-FLM***	**AF-FLM***	**AF-FLM***	
	AF-IF*	**AF-IF***	**AF-IF***	
	AF-IM	AF-IM	AF-IM	
	AF-UFM*	AF-UFM	AF-UFM	
	FLM-IF*	**FLM-IF***	**FLM-IF***	
	FLM-IM	FLM-IM	**FLM-IM***	
	FLM-UFM*	**FLM-UFM***	FLM-UFM	
	IF-IM	IF-IM	IF-IM	
	IF-UFM*	**IF-UFM***	**IF-UFM***	
	IM-UFM*	IM-UFM	IM-UFM	

Table III: Variation in nutritional intake among age-sex classes during high and low fruit periods. Data represent the mean ± SE (min-max). Fruit periods are based on the 50% quartiles for FAI. For adult females, data in brackets indicate expenditure estimates that do not incorporate additional reproductive costs. N = full-day follows. *Pontzer et al., 2010; †Key and Ross, 1999; ‡Harrison et al., 2010

	Adult females		Adult flanged males	
	High fruit (N=647)	Low fruit (N=747)	High fruit (N=115)	Low fruit (N=144)
Active period (min)	650.27 ± 2.34 (320 - 802)	648.43 ± 2.41 (294 - 794)	621.65 ± 6.42 (467 - 757)	615.69 ± 6.53 (326 - 770)
Daily feeding time (min)	354.52 ± 3.85 (28 - 648)	385.84 ± 3.23 (16 - 628)	317.98 ± 9.39 (122 - 534)	343.51 ± 7.16 (124 - 578)
Total energy intake (Kcal/day)	3199.32 ± 52.36 (286.13 - 7632.66)	2847.67 ± 60.33 (11.4 - 7995.66)	3052.9 ± 135.63 (455.58 - 7544.3)	2601.38 ± 114.98 (321.45 - 7013.06)
Available protein intake (g/day)	59.97 ± 1.25 (3.91 - 218.44)	65.41 ± 1.25 (0.24 - 207.62)	65.72 ± 4.22 (10.88 - 226.37)	68.52 ± 2.83 (12.55 - 187.32)
Lipid intake (g/day)	58.94 ± 1.9 0 (2.68 - 354.89)	59.69 ± 2.45 (0.13 - 389.09)	45.84 ± 4.28 (1.4 - 244.87)	50.34 ± 4.82 (3.78 - 302.09)
NDF intake (g/day)	578.19 ± 11.69 (21.02 - 1770.09)	471.1 ± 11.69 (4.14 - 1705.91)	605.82 ± 34.88 (53.9 - 1777.19)	442.56 ± 23.10 (59.02 - 1710.2)
TNC intake (g/day)	450.81 ± 8.65 (28.36 - 1364.85)	374.19 ± 8.99 (1.53 - 1281.19)	441.06 ± 21.24 (39.21 - 1066.66)	343.64 ± 17.46 (48.67 - 1050.78)
DM intake (g/day)	1232.03 ± 20.52 (88.81 - 2819.62)	1053.7 ± 21.67 (6.93 - 3032.98)	1250.92 ± 60.22 (165.9 - 3278.4)	989.46 ± 42.69 (153.79 - 3028.61)
Total # months	92		54	
Requirement DEE*	2153 [1435]		1861	
# months energy intake < DEE*	13 [4]		10	
% months energy intake < DEE*	18.5 [4.3]		18.5	
Requirement TDEE†; ‡	1898 [1448]; 1822 [1310]		2643; 2372	
% months energy intake < TDEE†	14.1 [4.4]		38.9	
% months energy intake‡ < TDEE† using ME (low)	89.7 (64.1)		92.1	

Table III, continued:

	Adult unflanged males		Immature independent females	
	High fruit (N=128)	Low fruit (N=89)	High fruit (N=138)	Low fruit (N=251)
Active period (min)	676.56 ± 4.97 (474 - 786)	671.28 ± 6.72 (444 - 808)	661.84 ± 4.80 (421 - 792)	659.87 ± 3.49 (405 - 794)
Daily feeding time (min)	337.89 ± 7.25 (108 - 568)	385.46 ± 9.68 (190 - 626)	378.87 ± 7.15 (126 - 534)	405.4 ± 4.43 (186 - 634)
Total energy intake (Kcal/day)	3208.03 ± 119.55 (303.48 - 6857.4)	2806.68 ± 157.83 (768.79 - 7003.25)	3239.87 ± 113.53 (584.66 - 6381.46)	2734.92 ± 91.24 (261.79 - 7616.51)
Available protein intake (g/day)	65.79 ± 3.35 (4.18 - 176.33)	79.18 ± 3.26 (26.98 - 155.71)	61.91 ± 2.67 (12.56 - 226.56)	65.84 ± 2.11 (5.02 - 176.9)
Lipid intake (g/day)	68.67 ± 4.70 (1.66 - 274.46)	43.44 ± 4.76 (4.34 - 223.29)	61.59 ± 3.95 (3.09 - 261.72)	47 ± 3.08 (1.83 - 365.28)
NDF intake (g/day)	523.12 ± 24.61 (75.39 - 1552.49)	502.51 ± 28.09 (131.13 - 1267.31)	537.03 ± 21.86 (106.45 - 1548.78)	480.83 ± 18.04 (48.35 - 1448.6)
TNC intake (g/day)	425.96 ± 17.2 (55.49 - 1013.04)	398.63 ± 30.94 (71.23 - 1413.17)	450.56 ± 19.46 (97.85 - 1276.85)	375.01 ± 15.44 (30.22 - 1318.97)
DM intake (g/day)	1172.17 ± 45.74 (144.1 - 2847.3)	1122.38 ± 57.68 (377.13 - 2441.82)	1192.02 ± 41.55 (242.38 - 2917.15)	1051.2 ± 34.56 (109.63 - 2863.37)
Total # months	53		71	
Requirement DEE*	1456		1207	
# months energy intake < DEE*	5		5	
% months energy intake < DEE*	10.6		7.0	
Requirement TDEE†;‡	1498; 1459		970	
% months energy intake < TDEE†	9.4		4.2	
% months energy intake‡ < TDEE† using ME (low)	60.9		--	

Table III, continued:

	Immature independent males	
	High fruit (N=39)	Low fruit (N=18)
Active period (min)	648.9 ± 8.34 (511 - 742)	625.41 ± 16.97 (519 - 732)
Daily feeding time (min)	310.72 ± 16.78 (22 - 538)	397.22 ± 19.83 (164 - 508)
Total energy intake (Kcal/day)	2831.76 ± 225.75 (162.81 - 7617.01)	3733.68 ± 394.72 (865.05 - 7418.4)
Available protein intake (g/day)	48.4 ± 3.87 (3.1 - 118.07)	70.21 ± 6.78 (36.33 - 125.6)
Lipid intake (g/day)	51.77 ± 7.22 (0.31 - 182.22)	54.43 ± 11.72 (8.22 - 222.28)
NDF intake (g/day)	568.09 ± 56.78 (13.27 - 1623.26)	555.73 ± 79.8 (124.17 - 1192.24)
TNC intake (g/day)	418.11 ± 38.57 (33.36 - 1172.49)	602.17 ± 58.05 (102.33 - 1037.44)
DM intake (g/day)	1153.79 ± 99.84 (54.06 - 2705.37)	1384.52 ± 149.17 (325.79 - 2639.54)
Total # months	21	
Requirement DEE*	1306	
# months energy intake < DEE*	3	
% months energy intake < DEE*	14.3	
Requirement TDEE†;‡	1163	
% months energy intake < TDEE†	9.5	
% months energy intake‡ < TDEE† using ME (low)	--	

Table IV: Percentage of time spent feeding different plant items among age-sex classes during low, middle, and high fruiting periods based on 9,630 full-day focal follows. Low, medium, and high fruit periods are based on statistical quartiles.

Food	Adult females			Flanged males			Unflanged males		
	Low	Medium	High	Low	Medium	High	Low	Medium	High
Inner bark (BK)	10.80	1.25	0.61	4.23	0.22	1.25	8.00	2.05	1.09
Ficus (FIG)	4.95	1.60	1.60	4.32	1.56	1.60	2.02	1.42	2.88
Flowers (FL)	9.15	10.88	1.88	4.71	16.75	10.88	13.91	10.48	3.83
Non-fig fruit (FR)	41.24	64.11	76.19	35.78	62.24	64.11	44.50	65.06	66.41
Insects (INS)	4.56	5.14	5.67	1.25	5.08	5.14	2.03	3.44	1.40
Mature leaves (LV)	2.24	3.19	2.06	6.66	1.38	3.19	2.09	1.93	2.00
Non-woody pith (PITH)	3.55	1.13	0.64	8.95	0.76	1.13	4.04	0.46	0.71
Other vegetation (VEG)	4.91	1.97	1.38	4.21	0.76	1.97	3.09	0.93	1.81
Young leaves (YL)	18.60	10.74	9.97	29.90	11.25	10.74	20.30	14.23	19.88

Food	Immature females			Immature males			Overall			
	Low	Medium	High	Low	Medium	High	Average	Low	Medium	High
Inner bark (BK)	9.77	2.22	0.28	0.00	0.00	0.00	3.88	9.72	1.32	0.57
Ficus (FIG)	3.36	1.62	0.85	3.77	0.96	0.00	2.45	4.32	1.56	1.51
Flowers (FL)	10.42	13.00	0.64	0.00	0.00	0.00	8.6	9.3	11.44	1.91
Non-fig fruit (FR)	48.70	56.94	75.09	66.50	82.38	66.50	59.22	43.01	63.44	74.18
Insects (INS)	7.25	8.23	10.79	0.11	5.31	15.58	5.28	4.67	5.52	5.65
Mature leaves (LV)	1.65	1.38	1.32	3.71	0.74	0.29	2.44	2.47	2.48	2.31
Non-woody pith (PITH)	3.90	1.14	0.26	0.40	0.26	0.78	1.88	4.05	1	0.52
Other vegetation (VEG)	2.56	3.41	1.38	7.48	1.49	0.29	2.56	4.23	1.98	1.3
Young leaves (YL)	12.39	12.06	9.39	18.04	8.86	16.55	13.69	18.22	11.26	12.05

RESEARCH HIGHLIGHTS

The spatial and temporal variation in food abundance has strong effects on wildlife feeding and nutrition. Here we present the first long term study of the effects of variation in fruit availability and age/sex class on nutritional ecology of wild Bornean orangutans. We examined variation in nutrient intake of wild orangutans in living in a peat swamp habitat over a 7-year period at the Tuanan Orangutan Research Station in Central Kalimantan. We conducted 2,316 full-day focal follows on 62 habituated orangutans (*Pongo pygmaeus wurmbii*). We found differences in total energy and macronutrient intake across age-sex classes, controlling for metabolic body mass. Intake of both total energy and macronutrients varied with fruit availability, and preference of dietary items increased with their nutritional quality. Foraging-related variables, such as day journey length, travel time, and feeding time, also varied among age-sex classes and with fruit availability. Our results add to the growing body of literature suggesting that great variation in foraging strategies exists among species, populations, and age-sex classes and in response to periods of resource scarcity.